EUHYSTRICHOCERAS AND *ALGERICERAS*, THE LAST MORTONICERATINE AMMONITES

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ABSTRACT. *Euhystrichoceras* Spath, 1923, *Algericeras* Spath, 1925, of which *Prionocycloides* Spath, 1925 is regarded as a synonym and *Sakondryella* Collignon, 1964 a subgenus, are the last, Cenomanian, members of the typically Upper Albian subfamily Mortoniceratinae. They are believed to have evolved from the diminutive *Cantabrigites* Spath, 1932 and are diminutive taxa of paedomorphic origin. The type and other poorly understood species are revised and a new species, *Euhystrichoceras baylissi*, the largest and youngest known, is described from the Upper Cenomanian of Devon.

THE widespread late Albian and early Cenomanian Tethyan faunas of small pyritic and limonitic ammonites described by Pervinquière (1907, 1910), Collignon (1928–1929, 1931, 1964) and others include both genuinely diminutive species and the nuclei of larger forms. Among the former is a small number of species with an entire keel or row of closely spaced siphonal clavi. Spath (1923) introduced the genus *Euhystrichoceras*, based on Coquand's species *Ammonites nicaisei*, and subsequently (1933) named two new species (*E. simplex* and *E. constrictum*) from England. In 1925 he based two further genera, *Algericeras* and *Prionocycloides*, on other species of Coquand which had been refigured by Pervinquière (1907, 1910). All three genera were referred to the Schloenbachiidae. Spath (1933, p. 438) later expressed some doubt as to this position in the case of *Algericeras* and *Prionocycloides* but regarded *Euhystrichoceras* as certainly a schloenbachiid. Since this time the position and affinities of these genera have remained puzzling. In the *Treatise* (p. L 400) *Euhystrichoceras* and *Prionocycloides* were retained in the Schloenbachiidae, with the remark that the latter 'was conceivably an acanthoceratid'. *Algericeras* (p. L 409) was placed in the Brancoceratidae (Mortoniceratinae) on the grounds that it was 'similar to and perhaps derived from *Cantabrigites*', as Spath had already pointed out (1933, p. 438).

Schloenbachiidae in the opinion of Spath (*passim*) and Wright (1957) included, besides the type genus and those already mentioned, several other little-known genera united only by the presence of a keel. Of these *Pseudacompsoceras* is a synonym of *Acompsoceras* Spath, 1925 (Acanthoceratidae) as shown by Casey (1965, p. 426). *Tropitoides* Spath, 1925 has a suture that suggests attribution to the Haploceratoceae and *Prohauericeras* Nowak, 1913 is of doubtful affinity (the genus was based on *Ammonites goupilianus* d'Orbigny, 1841; the types are lost and no other specimens have so far been recognized).

Schloenbachia Neumayr, 1875 is a well characterized genus, undoubtedly derived from the late Albian *Pleurohoplites–Lepthoplites–Callihoplites–Arrhaphoceras* complex of the Upper Albian *Stoliczkaia dispar* Zone by elevation of the rounded venter into a thin, high keel. As with the Hoplitidae, the genus has a generally Boreal distribution (Owen 1971, Juignet and Kennedy 1976, fig. 20), extending no further south than south-eastern France, Transcaspia, and Iran north of the Zagros (Kennedy *et al.* 1979). This is so different from the largely Tethyan occurrence of *Euhystrichoceras* and its allies that on biogeographical criteria alone we came to suspect the affinities of the group. We now suggest that these ammonites are diminutive members of the Mortoniceratinae. This is based on an examination of the type specimens, or in some cases plaster casts, of the types of all the taxa discussed.

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LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of specimens cited in the text: BMNH—British Museum (Natural History), London; MNHP—Muséum d'Histoire Naturelle, Paris; SP—Sorbonne Collections, now housed in the Université de Paris VI; UCBS—Palaeontology Department, Berkeley, California; UT—University of Texas Collections, Austin.

SUTURE TERMINOLOGY AND DIMENSIONS

The suture terminology is that of Wedekind (1916), reviewed by Kullman and Wiedmann (1970): E = external lobe, L = lateral lobe, U = umbilical lobe, I = internal lobe. All dimensions are given in millimetres, figures in parentheses being the dimensions as a percentage of the total diameter. D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus, B = umbilical bullae on outer whorl; R = ribs on outer whorl.

SYSTEMATIC PALAEONTOLOGY

Superfamily ACANTHOCERATACEAE Grossouvre, 1894
Family BRANCOCERATIDAE Spath, 1925
Subfamily MORTONICERATINAE H. Douvillé, 1912
Genus EUHYSTRICHOCERAS Spath, 1923

1923 *Euhystrichoceras* Spath, p. 143.

Type species. *Ammonites nicaisei* Coquand, 1862 p. 323, pl. 35, figs. 3, 4, by the original designation of Spath, 1923 p. 143.

Diagnosis. Small (largest-known individual has an estimated diameter of only 50 mm); evolute to moderately involute with depressed rounded to compressed quadrate whorls. Inner whorls with strong to weak umbilical tubercles that give rise to groups of two or three straight to flexuous ribs with additional shorter intercalated ribs. Body-chambers may be densely and flexuously ribbed, with weakening bullae. Ventral clavi are present in some species, in which lautiform ribbing may develop. The venter has a strong entire keel. The suture line is very simple, with narrow, little incised lobes and broader, bifid saddles.

Discussion. The genus was not diagnosed by Spath when it was established. In 1933 (p. 439) he merely referred to 'the simplified, almost *Brancoceras*-like suture-line'. In fact the suture-line is much like that of uppermost Albian *Cantabrigites* as figured by Spath (1933, pl. 45, fig. 4; pl. 46, fig. 11*a*, *b*)

EXPLANATION OF PLATE 59

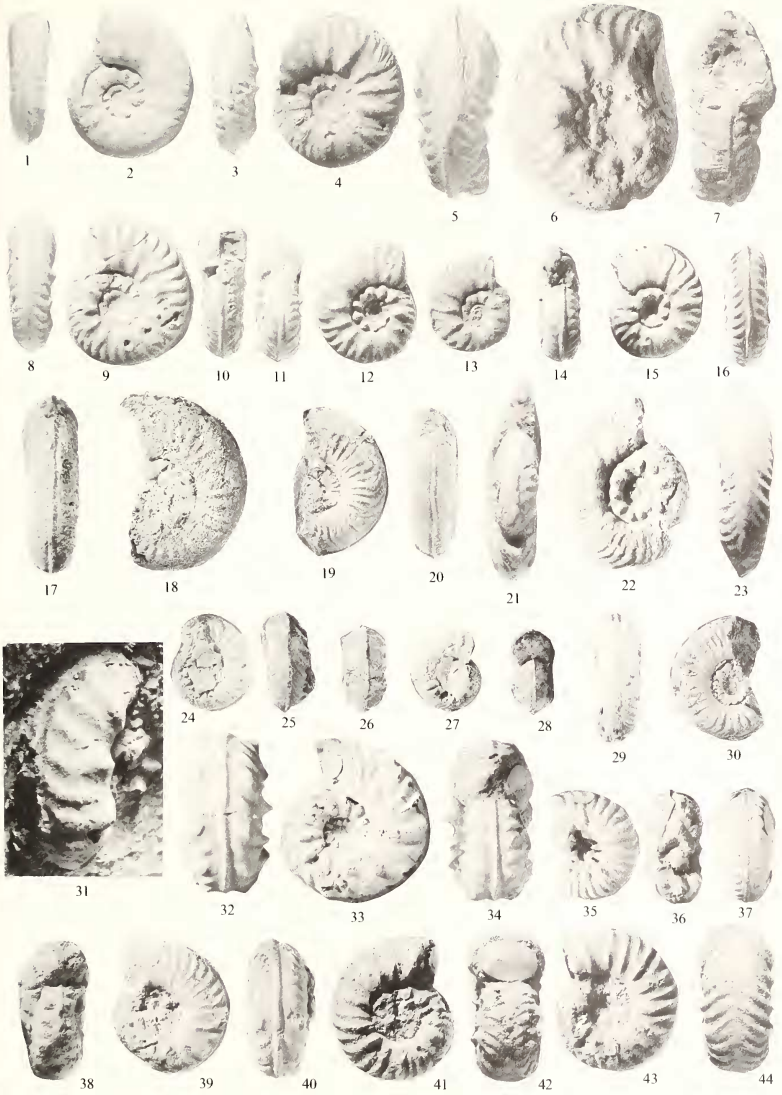
Figs. 1–16, 21–23. *Euhystrichoceras nicaisei* (Coquand). 1–2, the original of Pervinquière 1910, pl. 15, fig. 10; 3–4, pl. 15, fig. 8; 5–7, pl. 15, fig. 9; 8–10 the lectotype, pl. 15, fig. 7; 13 is pl. 15, fig. 6. All specimens from west of Boghar, Tunisia. 11, 12, original of Pervinquière, 1910, pl. 15, figs. 18, 19*a–c* from Dahlia, Algeria; 14–16, original of Pervinquière 1910, pl. 15, figs. 15, 16*a–b*, from Djebel Guessa, Algeria. 21–23, original of Pervinquière, 1910, pl. 15, figs. 11*a–b*, 12*a–b*, from Aumale, Algeria. All figures are × 2.

Figs. 17–20, 24–30. *Euhystrichoceras adkinsi* Powell. Topotypes from the Ojinaga Formation (Bed A of Powell 1963), Love Station, Jeff Davis County, West Texas. 17–18 are BMNH C80934; 19–20 are C80937; 24–25 are C80941; 26–28 are C80940; 29–30 are C80933. All figures are × 2.

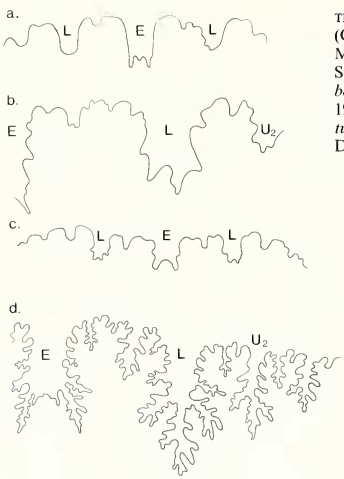
Fig. 31. *Euhystrichoceras occidentale* Reyment. Holotype, BMNH C3534, from the Odukpani Formation of Nigeria. × 2.

Figs. 32–34, 38–40. *Euhystrichoceras constrictum* Spath. 32–34, the holotype, BMNH 88694 from Warminster, Wiltshire; 38–40, WW 21349, from Rocken End, Isle of Wight, Hampshire. All figures × 1.

Figs. 35–37, 42–43. *Euhystrichoceras simplex* Spath. 35–37, the holotype, BMNH 37276, from Warminster, Wilshire; 41–44, BMNH C80932 (ex. H. G. Owen Collection), from Woody Bay, Ventnor, Isle of Wight, Hampshire. All figures × 1.



KENNEDY and WRIGHT, *Euhystrichoceras*



TEXT-FIG. 1. External sutures of: a. *Euhystrichoceras nicaisei* (Coquand) (original of Pervinquière 1907, pl. 6, fig. 12). ×6. Mature, but not terminal suture. b. *Cantabrigites cantabrigiense* Spath (original of Spath 1933, pl. 45, fig. 4). ×3. c. *Algericeras boghariense paucicostatum* subsp. nov. (original of Pervinquière 1910, pl. 15, fig. 28). ×6. d. *Schloenbachia varians subtuberculata* (Sharpe). Taken from a juvenile from Wilmington, Devon. (OUM K10184). ×3.

but with one or two more auxiliary lobes (text-fig. 1); the two taxa are distinguished only by the more irregular and more persistently branching or long and short ribbing of *Euhystrichoceras*, its generally much less marked ventrolateral shoulders and consequently more rounded, less subquadrate whorl section and its less serpenticone coiling. Collignon (1964) introduced the subgenus *Euhystrichoceras* (*Sakondryella*) for a very variable new species, *E.* (*S.*) *madagascariensis*. He separated it from *Euhystrichoceras sensu stricto* because of the presence of a row of siphonal clavi rather than an entire keel, but, as shown below, this group is better referred to as a subgenus of *Algericeras*.

Occurrence. *Euhystrichoceras* is doubtfully recorded from the uppermost Albian (*Stoliczkaia dispar* Zone) of Switzerland (Renz 1968). It occurs widely in the Lower Cenomanian of Algeria, Tunisia, Madagascar, and Texas, where it is locally abundant. It occurs as a rarity in the Lower Cenomanian of Nigeria, Sarthe and Normandy in France and in southern England. A single specimen is known from the Upper Cenomanian in Devon, England.

Euhystrichoceras nicaisei (Coquand)

Plate 59, figs. 1–16, 21–23; text-figs. 1*a*, 2*d*

1862 *Ammonites nicaisei* Coquand, p. 323, pl. 35, figs. 3–4.
non 1968 *Euhystrichoceras* cf. *nicaisei* (Coquand); Renz, p. 64, pl. 11, fig. 7*a–b*.
1976 *Euhystrichoceras nicaisei* (Coquand); Juignet and Kennedy, p. 79, pl. 5, figs. 5*a–b*, 6*a–c* (with full synonymy).

Types. It is clear from Coquand's description that he had a series of specimens of this species before him, all from the Lower Cenomanian west of Boghar, Algeria, collected by a M. Nicaise. Pervinquière (1910, p. 10, figs. 6–10) refigured the surviving specimens in Coquand's collection (housed in the collections of the Geological Institute, Nepstadion Korut, Budapest) and plaster casts of these are before us (BMNH C80927–31; Pl. 59, figs. 1–10, 13). Juignet and Kennedy (1976, p. 80) designated the original of Pervinquière's (1910) pl. 6, fig. 7 lectotype of the species, and it is refigured here as Pl. 59, figs. 8–10.

Other material studied. Tunisian material figured and described by Pervinquière (1907, p. 235, pl. 11, figs. 13*a–b* to 15*a–c*), Algerian specimens described by the same author (1910, p. 65, pl. 15, figs. 11*a–b* to 19*a–c*), Madagascan specimens described by Collignon (1928–1929, p. 31, pl. 16, figs. 16, 16*a*; 1931, p. 74, pl. 3, figs. 16, 17).

Description. As noted by Pervinquière (1907, p. 235; 1910, p. 65) this species shows a wide range of variation, with both compressed and inflated individuals, showing a corresponding variation in rib and tubercle strength. On inner whorls, coiling is relatively involute, with a depressed inflated whorl section, the greatest breadth being at the conical umbilical tubercles. The outer flanks are flattened and convergent and the venter broad and flat with a strong siphonal keel, flanked by distinct grooves. There are generally six to ten inner lateral tubercles, linked to the umbilical seam by relatively strong, distant ribs (Pl. 59, figs. 12, 15). These give rise to pairs of narrower concave, prorsiradiate ribs which, together with intercalatories, sweep forwards across the ventrolateral shoulders to terminate at the grooves bounding the ventral keel. The chevron so formed is generally obtuse.

In slender individuals the umbilical tubercles are less conspicuous, the sides flatter and ribs weaker (e.g. Pl. 59, figs. 2, 9).

Specimens reach maturity at widely differing adult diameters ranging from 11·5 mm (Pl. 59, figs. 11–12) to 21 mm (Pl. 59, figs. 5–7). In the smaller adults the coiling becomes more evolute, the whorl section is less depressed, and the inner lateral tubercles decline. Ornament typically consists of distant bullate straight and prorsiradiate primary ribs which may branch at mid-flank and are accompanied by short intercalated ribs, all of which are concave on the outer flank and sweep forwards across the ventrolateral shoulder, thickening as they do so, and are then attenuated towards the ventral grooves. At the aperture long, simple primary ribs dominate and, in one intermediate sized specimen, flexuous primary ribs cover all the body-chamber (Pl. 59, fig. 22); in another (Pl. 59, fig. 2) ribbing is very subdued, although this is in part due to wear.

The largest adult (Pl. 59, figs. 5–7), in contrast, retains strong umbilical bullae throughout, connected to the umbilical seam by straight distant ribs and giving rise to groups of two or three concave ribs with additional intercalatories—retention, in other words of the juvenile ornament of the smaller adults. An intermediate form which has some body chamber is shown in Pl. 59, figs. 3–4. These rather different, apparently micro- and macromorph, adult forms may reflect dimorphism in the species, but there are inadequate data to make this certain.

The sutures are relatively simple, with a quite broad E which has a short, broad median element. E/L is broad, asymmetrically bifid or incipiently trifid and little incised; L/U_2 narrow and simple, U_2 much smaller and scarcely denticulate (text-figs. 1*a–2d*).

Discussion. Renz (1968) described and figured (p. 64, pl. 11, fig. 7*a, b*) as *Euhystrichoceras* cf. *nicaisei* (Coquand) a fragment of a body-chamber from the uppermost Albian *Stoliczkaia dispar* Zone of Sainte Croix, Switzerland. It is rather evolute and compressed with convex sides curving to a fastigiate venter; there are strong falcoid, branched or single ribs, continuing forwards over the ventro-lateral shoulders to join a crenulate keel. The general appearance resembles that of the body-chamber of the specimen of *E. nicaisei* in Pl. 59, figs. 21–23 but the ribbing is sharper. This fragment is certainly specifically distinct from *E. nicaisei* but, in the absence of ventrolateral tubercles, it is equally distinct from *Algericeras* (*Sakondryella*) described below. Better material is needed before one can decide where it stands in relation to the forms described in this paper.

Occurrence. Lower Cenomanian of Algeria, Tunisia, Madagascar, Sarthe and Normandy in France.

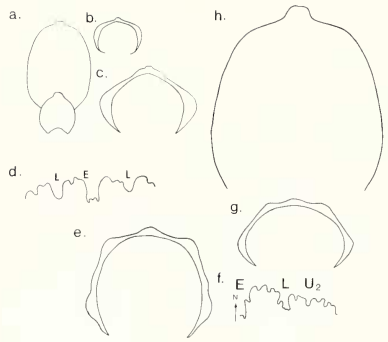
Euhystrichoceras adkinsi Powell

Plate 59, figs. 17–20, 24–30; text-fig. 2*a–c*.

1963 *Euhystrichoceras adkinsi* Powell, p. 311, pl. 31, figs. 2–6, 8; text-fig. 3*k*.

Holotype. UT 36217 from the lower part of the Ojinaga Formation (Bed A of Powell 1963), Love Station, 600 m south-east of U.S.C. and G.S. triangulation station 'Love' and 275 m south of the nose of a southward-plunging syncline, Hudspeth County, about 160 km south-east of El Paso, Texas.

Other specimens studied. Numerous topotypes, including a suite in the British Museum Collections (C 80933–51).



TEXT-FIG. 2. Sutures and whorl sections of *Euhystrichoceras* species. a–c. *Euhystrichoceras adkinsi* Powell. a, BMNH C80939; b, C80951; c, C80945. ×3. d. *Euhystrichoceras nicaisei* (Coquand). Original of Pervinquière 1907, pl. 6, fig. 12. ×3. e–g. *Euhystrichoceras constrictum* Spath. WW21349. ×1·5. h. *Euhystrichoceras baylissi* sp. nov. BMNH C82177. ×1·5.

Discussion. Powell had described this species in detail. The early whorls are depressed and coronate (Pl. 59, figs. 24–28) but adults are markedly compressed (Pl. 59, figs. 17–20, 29–30). On the phragmocone there are usually twenty to twenty-two primary ribs, strongly flared at mid-flank, where they bear a strong bulla (described by Powell as umbilical). From these bullae arise pairs of delicate prorsiradiate secondary ribs, and additional short ribs may be intercalated, giving a total of thirty-five to forty secondary ribs per whorl (Pl. 59, figs. 25, 26). On the body chamber the bullae weaken, secondary ribs are lost (Pl. 59, fig. 30) and ornament consists of dense, flexuous, prorsiradiate ribs. The keel is narrow, sharp, and high and, where well-preserved shell is present, can be seen to be minutely serrate.

Compressed whorls and dense, flexuous ribbing with loss of bullae, together with absence of irregular ventrolateral clavi immediately distinguish this species from *E.* (*E.*) *constrictum* (Pl. 59, figs. 32–34, 38–40). *E.* (*E.*) *simplex* is more inflated and coarsely ribbed, has the bullae much lower on the flank, and is much more evolute (Pl. 59, figs. 35–37, 41–44). *E.* (*E.*) *occidentale* (Pl. 59, fig. 31) is equally distinctive. In *E.* (*E.*) *nicaisei*, ribbing is coarser in adults and bullae, secondary and intercalatory ribs are often retained (e.g. Pl. 59, figs. 6, 9, 12).

Occurrence. Known only from the type locality, and probably of early Cenomanian date (Powell 1963, Young and Powell 1978).

Euhystrichoceras baylissi sp. nov.

Plate 60, figs. 25–26; text-fig. 2*h*

Holotype. A single fragment, BMNH C82177, formerly no. 1174 in the collections of Colonel O. H. Bayliss of Uplyme, Dorset, from the Upper Cenomanian phosphatic fauna of Division C of the Cenomanian Limestone of Shapwick Grange, Devon.

Description. The specimen is a phosphatic internal mould of one-third of a whorl of body chamber with a maximum whorl height of 20 mm, corresponding to an estimated diameter of at least 50 mm, making this the largest *Euhystrichoceras* known. Coiling appears to have been relatively evolute with a quite deep umbilicus of moderate size. The whorl section is compressed, with a breadth to height ratio of 0·86, the greatest breadth being some way below mid-flank (text-fig. 2*h*). The umbilical wall is flattened, sloping steeply outwards, with an abruptly rounded shoulder. The inner flanks are feebly convex, the outer flattened, with a broad, flattened venter. Six ribs arise at the umbilical seam, passing backwards across the umbilical wall to strengthen at the shoulder where they are sharp, narrow, and distant, without bullae. On the flank these ribs follow a prorsiradiate falcoid course, being straight across the inner flank, convex at mid-flank, and concave across the outer, where they broaden markedly. The ribs are projected strongly forwards across the ventrolateral shoulders, weakening

and attenuated as they do so, each almost joining the succeeding rib. Two primary ribs bifurcate below mid-flank, so that there is a total of ten ribs on the venter, the pattern of ornament being of alternating single and twin-bladed sickles. The ventral keel is strong, sharp, and high and bears traces of growth striae, linked to the ventrolateral ribs. The general appearance is very close to that of *Dipoloceras bouchardianum* (d'Orbigny) (1841, p. 300, pl. 138, figs. 6–8).

Discussion. This is the largest *Euhystrichoceras* known; in comparison the largest known *E. constrictum* is 30·4 mm in diameter and the largest known *E. nicaisei* only 20 mm. Because of these size differences comparisons with other species are difficult; indeed size alone serves to distinguish *E. baylissi* from all others. *E. adkinsi* has denser, flexuous simple ribs on the body-chamber and is more compressed. In *E. constrictum* there are convex to only very feebly flexed, rather irregularly long and short ribs on the body chamber, sometimes lautiform on the early part, and immediately distinctive lateral and ventral tubercles. *E. simplex* is a depressed species, with alternately long and short ribs on the body-chamber, the ribs prorsiradiate, straight on the inner flank and far less projected on the venter, producing a less acute chevron. *E. nicaisei* has somewhat variable body chambers; in slender forms the whorl section is much more compressed and ribs dense and delicate (Pl. 59, fig. 22); as inflation increases (Pl. 59, fig. 6) strong tubercles are retained, giving rise to pairs of ribs with occasional short intercalatories. The angle of the ventral chevron is also more obtuse. The tiny *E.* (*E.*) *occidentale* Reyment (Pl. 59, fig. 31) has strong umbilical bullae on the apparently adult body chamber. In summary, in spite of being known from a single fragment only, this specimen is distinguished from all others by size and ornament, as well as being later by more than half of the Cenomanian stage.

Occurrence. Upper Cenomanian of Devon, England.

Euhystrichoceras simplex Spath

Plate 59, figs. 35–37, 41–44.

1933 *Euhystrichoceras simplex* Spath, pl. 49, figs. 8*a–b*.
1951 *Euhystrichoceras simplex* Spath; Wright and Wright, p. 23.
1971 *Euhystrichoceras simplex* Spath; Kennedy, p. 46.
1976 *Euhystrichoceras simplex* Spath; Juignet and Kennedy, p. 80.

Holotype. BMNH 37276, from the Lower Cenomanian of Warminster, Wiltshire, *ex* J. Baker Collection. Other than the holotype, the only known specimen is BMNH C80932 (ex. H. G. Owen Collection), from the early Cenomanian Glauconitic Marl of Woody Point, Woody Bay, Isle of Wight, Hampshire.

Dimensions

	D	*Wb*	*Wh*	*Wb: Wh*	*U*
BMNH 37276	20·8 (100)	10·3 (49)	7·1 (34)	1·45	7·0 (34)
BMNH C80932	25·2 (100)	12·3 (49)	7·6 (30)	1·61	10·3 (41)

Description. The holotype is a well-preserved phosphatic irridescent mould retaining two-thirds of a whorl of body chamber. Coiling is moderately involute, with a quite deep umbilicus. The umbilical wall is high, sloping slightly outwards. The whorl section is depressed and rounded with the greatest breadth low on the flank in intercostal section and at the umbilical bulla in costal section. There are twenty-two ribs on the two-thirds of a whorl of body chamber preserved, corresponding to a total of seven small bullae at the umbilical shoulder. The ribs arise in pairs from the bullae or are intercalated low on the flank. All are narrow, rounded and separated by relatively wide interspaces. They are prorsiradiate and straight to gently flexed on the inner flank, but concave and projected strongly forwards over the ventrolateral shoulder to form an obtuse chevron over the venter, where they decline markedly on either side of the rather weak siphonal keel. The suture lines are not decipherable.

The second specimen referred to the species shows sutural crowding and possesses two-thirds of a whorl of body chamber, appearing to be adult. It has much stronger umbilical bullae on the phragmocone than the holotype, but shows a similar style and grouping of ribs. On the body-chamber the ribbing simplifies and the aperture is simple and entire. There is a distinct but very low rounded keel on the phragmocone, which virtually disappears on the body-chamber, on which the chevrons formed by the ribs on the venter are barely interrupted.

Discussion. *E.* (*E.*) *simplex* differs markedly at first sight from *E.* (*E.*) *nicaisei* in its depressed, coronate body-chamber and reduced keel. However the inner whorls are little, if any, more depressed than those of some specimens of *nicaisei*. Moreover the body-chambers of most of Pervinquière's specimens of *nicaisei* are more or less crushed. We think it likely that, if more material were available, *simplex* would be found to be based on no more than the inflated extremes of a single variable species, *nicaisei*. It is, however, possible that the populations from England and North Africa will be found not to overlap. In the absence of adequate samples to determine the extent of variation we provisionally maintain *simplex* as a separate species.

Occurrence. Lower Cenomanian of Wiltshire and the Isle of Wight, Hampshire, England.

Euhystrichoceras (*Euhystrichoceras*) *constrictum* Spath

Plate 59, figs. 32–34, 38–40; text-fig. 2*e–g*

1933 *Euhystrichoceras constrictum* Spath, pl. 49, fig. 9*a–b*; text-fig. 160*i*.
1951 *Euhystrichoceras constrictum* Spath; Wright and Wright, p. 23.
1971 *Euhystrichoceras constrictum* Spath; Kennedy, p. 46.
1976 *Euhystrichoceras constrictum* Spath; Juignet and Kennedy, p. 80.

Holotype. BMNH 88694, from the early Cenomanian of Warminster, Wiltshire, *ex* Cunnington Collection. Apart from the holotype, the only other specimen known is WW 21349, from the Lower Cenomanian Glauconitic Marl of Rocken End, Isle of Wight, Hampshire.

Dimensions

	D	*Wb*	*Wh*	*Wb*: *Wh*	*U*
BMNH 88694	30·4 (100)	13·8 (45)	10·7 (33)	1·3	10·3 (34)
at	24·5 (100)	12·5 (51)	9·5 (31)	1·26	8·8 (36)
WW 21349	24·5 (100)	7·8 (32)	8·5 (35)	0·92	7·8 (32)

EXPLANATION OF PLATE 60

Figs. 1–5, 20–24, 33. *Algericeras* (*Algericeras*) *proratum* (Coquand). 1–2, the originals of Pervinquière 1907, pl. 11, fig. 7, from Guern er Rhezal, Tunisia. 3, 4 are from the same locality; 5 is the original of Pervinquière 1910, pl. 15, fig. 26, from Aumale, Algeria. Figs. 20–21 are the originals of Pervinquière 1910, pl. 15, figs. 25*a–b*, from Aumale, Algeria; 22–24, the original of Pervinquière 1907, pl. 11, figs. 9*a–b*, from Guern er Rhezal, Tunisia; 33 is from Guern er Rhezal, Tunisia. All from the Collections of the Sorbonne, Paris. All figures × 2.

Figs. 7–8. *Algericeras bogharíense bogharíense* (Coquand). The original of Pervinquière 1907, pl. 11, figs. 16*a–b*, from Sidi Youssef, Tunisia, Sorbonne Collections. All figures × 2.

Figs. 9–19, 27–29. *Algericeras bogharíense paucicostatum* subsp. nov. 9–10, from Si Abd el Kerim, Tunisia. 11–13, the originals of Pervinquière 1910, pl. 15, fig. 28, from Aumale, Algeria. 14–16, holotype, the original of Pervinquière 1910, pl. 11, figs. 10*a–b*, from Guern er Rhezal, Tunisia. 17–19, the original of Pervinquière 1910, pl. 11, figs. 11*a–b*, from Si Abd el Kerim, Tunisia. 27–29, the original of Pervinquière 1907, pl. 11, fig. 12, from Si Abd el Kerim, Tunisia. All figures × 2.

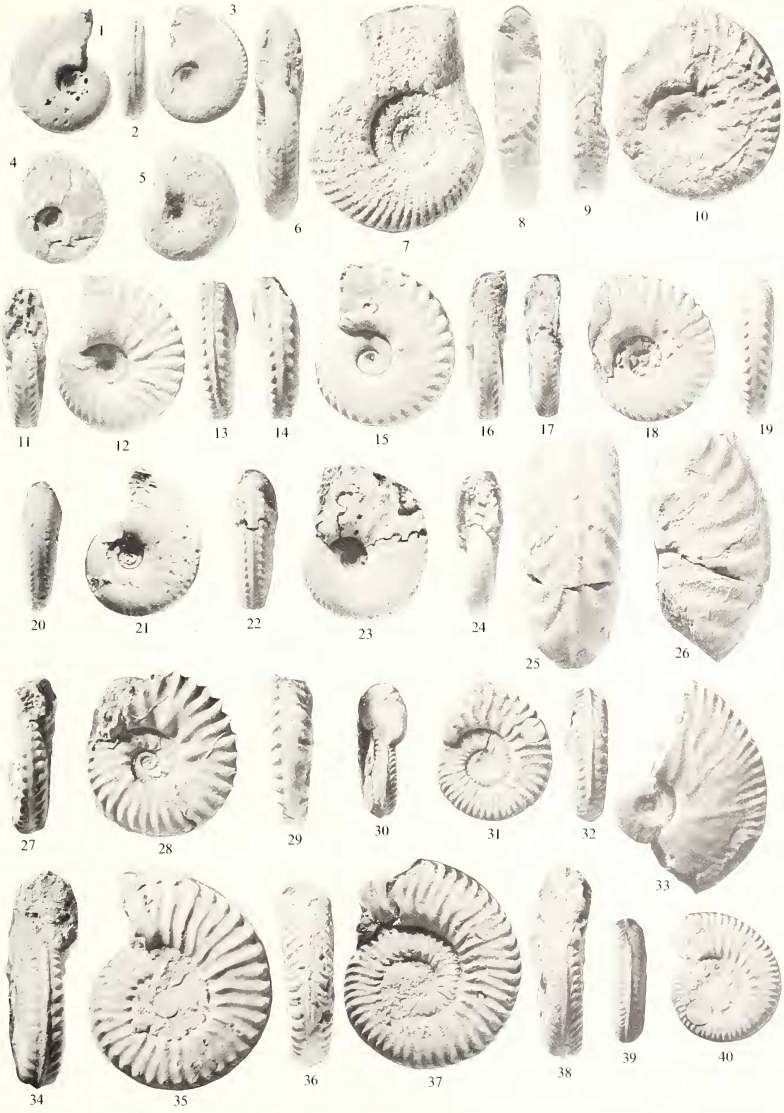
Figs. 25–26. *Euhystrichoceras baylissi* sp. nov. The holotype from Bed C of the Cenomanian Limestone at Shapwick Grange, Devon. BMNH C82177. × 1.

Figs. 30–32. *Cantabrigites cantabrigiense* Spath. BMNH C35854, from the Cambridge Greensand. × 1.

Figs. 34–35. *Cantabrigites subsimplex* Spath. Holotype, BMNH C35841, from the Cambridge Greensand. × 1.

Figs. 36–38. *Cantabrigites cantabrigense* Spath. Holotype, SMC 81, from the Cambridge Greensand. × 1.5.

Figs. 39–40. *C. cantabrigense gracile* Spath. BMNH 68497, from the Cambridge Greensand. × 1.



KENNEDY and WRIGHT, *Algericeras*, *Euhystrichoceras* and *Cantabrigites*

Description. The holotype is a well-preserved phosphatic irridescent mould of an adult specimen with two-thirds of a whorl of body-chamber preserved. Coiling is moderately evolute, with a quite deep umbilicus. The umbilical wall slopes outwards and the shoulder is rounded, merging imperceptibly with the strongly rounded inner flank. The whorl section is depressed on the phragmocone, with the maximum breadth at or about mid-flank in intercostal section and at the strong lateral bullae in costal section. The costal section is polygonal. Ornament consists of thirteen primary ribs to a whorl. These arise at the umbilical seam as mere striae and strengthen across the wall and shoulder into narrow, high, distant ribs. Each bears a strong lateral tubercle, bullate on the early whorls but becoming stronger and conical as size increases.

From each tubercle pairs of narrow, high, convex, prorsiradiate ribs arise and sweep across the outer flanks and ventrolateral shoulder. At the smallest diameter visible, these ribs terminate in an obliquely placed ventral tubercle (Pl. 59, fig. 33), separated by a smooth ventral band from the strong siphonal keel. As size increases, this tuberculation differentiates and alternate ribs bear strong and very weak, or no, tubercles. On the first half of the body-chamber the attitude of the tubercles changes from oblique to parallel to the keel and they elongate into clavi, which may link pairs of ribs in lautiform fashion (Pl. 59, fig. 33), with up to three nontuberculate ribs between successive tuberculate ones. There are three crowded ribs without lateral or ventral tubercles immediately preceding the somewhat contracted adult aperture, which lacks lateral processes but is projected into a short blunt rostrum. The suture line is very simple with broad, little incised bifid lobes and narrower saddles.

The second specimen referred to the species is significantly smaller than the holotype. It shows the same development of ventral clavi and lautiform ribbing on the early parts of the body-chamber (Pl. 59, figs. 38–40), but thereafter (Pl. 59, fig. 39) all tubercles are lost, and ornament consists of dense, narrow, flexuous prorsiradiate ribs which arise at, or just outside the umbilical seam.

Discussion. The coronate early whorls with bullae at mid-flank are reminiscent of *Euhystrichoceras adkinsi* (e.g. Pl. 59, figs. 24–28), but the ribbing is much coarser. At larger sizes, lautiform ribbing and the strong, irregular ventrolateral clavi distinguish it readily from all other species referred to the genus.

Occurrence. Lower Cenomanian of the Isle of Wight, Hampshire and Warminster, Wiltshire.

Euhystrichoceras occidentale Reyment

Plate 59, fig. 31

1955 *Euhystrichoceras occidentale* Reyment, p. 19, pl. 2, figs. 4, 5; text-fig. 8.

Types. The holotype is BMNH C48837 from the early Cenomanian Odukpani Formation 4·4 km north of Odukpani, Nigeria; there is also a small paratype fragment, BMNH C48857.

Discussion. This species is based on two tiny scraps, well-illustrated by Reyment (1955, pl. 2, figs. 4, 5). The smaller paratype, BMNH C48857, has a whorl breadth of only 5 mm and bears only six ribs, but already the strong distant bullate primary ribs separated by several intercalatories, better shown in the holotype, are visible. The holotype is a body-chamber fragment (Pl. 59, fig. 31). This seems to be a distinct species with coarser, thicker, and less flexuous ribs on the body-chamber, but it is not well enough known for adequate comparison to be made with other species.

Genus ALGERICERAS Spath, 1925

1925 *Algericeras* Spath p. 182

Type species. Ammonites boghariensis Coquand, 1879, p. 32 by original designation.

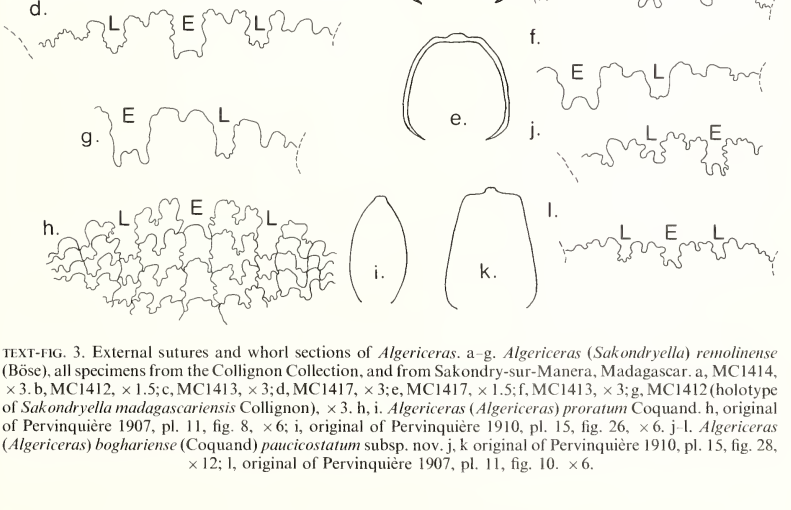
Diagnosis. Small forms, rather evolute to rather involute, very compressed to inflated and depressed, with regular or irregular umbilical bullae, straight or sinuous, recti- or prorsiradiate, fine or coarse ribs ending in fine ventrolateral tubercles and with a keel either nodate at first then entire or nodate throughout. The suture has feebly indented or entire elements, tending to be pseudoceratitic.

Discussion. Spath did not diagnose or describe his genus *Algericeras* when he established it and in later discussion only made allusions to its suture line. Moreover he did not differentiate it in any way

from *Prionocycloides*, established at the same time, or from *Euhystrichoceras*, set up two years earlier. In considering these three taxa, together with *Sakondryella*, established by Collignon (1964) as a subgenus of *Euhystrichoceras*, we have to select which features should be given the greatest importance.

Euhystrichoceras Spath, 1923 has in general a rounded whorl section, depressed from an early stage, and a rounded venter; it is rather evolute; the ribs are mostly sinuous and strongly projected on the shoulders; ventrolateral tubercles, if present, occur only on the inner whorl; the keel is entire throughout (although in *E. adkinsi* it is crossed by fine striae). *Sakondryella* Collignon, 1964 has a whorl section varying from rather compressed with slightly convex sides to inflated and depressed, with flat or rounded venter; it is slightly evolute; the ribs are strong, straight or flexed, slightly projected on the shoulders or not, normally with rounded tubercles; the keel consists of a row of rounded tubercles on a slight ridge throughout. *Algericeras* Spath, 1925 has a compressed whorl section, flat sided with tabulate or rounded/fastigiate venter and is rather evolute; the ribs are moderately strong, straight or slightly flexuous, with small oblique ventrolateral tubercles from an early stage; they branch from umbilical bullae or slightly higher up the side or are long and short; the keel is at first a row of siphonal nodes and later entire. *Prionocycloides* Spath, 1925 has a compressed whorl section with slightly convex sides and a subtabulate to rounded venter and is rather involute; the ribs are weak, sinuous to biconcave, bidichotomous and there are very fine oblique ventrolateral tubercles; the keel is a row of siphonal nodes at first and later entire.

The differences between *Algericeras* and *Prionocycloides* seem very slight in contrast to the similarities in keel, venter, and general build. We feel bound to regard the differences between *boghariense* and *proratus*, the type species of the two taxa, as no more than specific. The compressed



TEXT-FIG. 3. External sutures and whorl sections of *Algericeras*. a–g. *Algericeras* (*Sakondryella*) *remolinense* (Böse), all specimens from the Collignon Collection, and from Sakondry-sur-Manera, Madagascar. a, MC1414, ×3. b, MC1412, ×1.5; c, MC1413, ×3; d, MC1417, ×3; e, MC1417, ×1.5; f, MC1413, ×3; g, MC1412 (holotype of *Sakondryella madagascariensis* Collignon), ×3. h, i. *Algericeras* (*Algericeras*) *proratum* Coquand. h, original of Pervinquière 1907, pl. 11, fig. 8, ×6; i, original of Pervinquière 1910, pl. 15, fig. 26, ×6. j–l. *Algericeras* (*Algericeras*) *boghariense* (Coquand) *paucicostatum* subsp. nov. j, k original of Pervinquière 1910, pl. 15, fig. 28, ×12; l, original of Pervinquière 1907, pl. 11, fig. 10. ×6.

members of *Sakondryella* are only slightly more inflated than some of the new subspecies of *Algericeras boghariense* described below, have similar ribbing and tuberculation on the sides, and differ only in the persistent nodate keel. On the other hand, *Euhystrichoceras* differs from all the others in having no nodate keel and no ventrolateral tubercles except on the body-chamber, in its broadly rounded venter and, in some species, very irregular ribbing. It is, in our view, reasonable to treat *Sakondryella* as a subgenus within *Algericeras*, thus grouping together all the forms with a keel that is nodate at any stage and that have basically similar ribbing and tuberculation.

Occurrence. Lower Cenomanian of Algeria, Tunisia, Madagascar and Mexico.

Subgenus ALGERICERAS sensu stricto
(= *Prionocycloides* Spath, 1925)

Diagnosis. Keel nodate at first, later entire.

Algericeras (*Algericeras*) *boghariense* (Coquand).

Plate 60, figs. 6–19, 27–29; text-figs. 3, 4

Description. Compressed, slightly involute to slightly evolute, with more or less flat sides and tabulate to fastigiate venter with a keel nodate at first, but tending to become entire. Thin regular or alternately weak and strong oblique bullae on the umbilical shoulder give rise to more or less sinuous ribs in twos or threes or primaries with one or two shorter secondaries. Two subspecies are recognized.

Algericeras (*Algericeras*) *boghariense boghariense* (Coquand)

Plate 60, figs. 6–8

1862 *Ammonites favrei* Coquand, p. 172, pl. 2, figs. 3–4 (*non* Ooster).
1879 *Ammonites Boghariensis* Coquand, p. 35.
1907 *Mortoniceras Boghariensis* Coq.; Pervinquière, p. 240, pl. 11, fig. 16*a–b*.
1910 *Mortoniceras* (?) *Boghariense* Coq.; Pervinquière, p. 67, pl. 6, figs. 29–32; text-fig. 32.
1920 *Mortoniceras boghariense* Coquand; Stieler, p. 93.
1925 *Algericeras boghariense* (Coquand); Spath, p. 182.
1931 *Schloenbachia* (*Inflaticeras*) aff. *boghariense* Coquand; Collignon, p. 35, pl. 3, figs. 19–19*b*.
1933 *Algericeras boghariense* (Coquand); Spath, p. 437.
1957 *Algericeras boghariense* (Coquand); Wright, p. L 409.

Types. The syntypes are the four specimens from Berrouaghia, Algeria in the Coquand Collection, now housed in Budapest, figured by Pervinquière (1910, pl. 15, figs. 29–32). Of these we here select the original of Pervinquière's figure 30, which is probably the specimen figured by Coquand in 1862 as his pl. 2, figs. 3–4, as lectotype.

Material studied. In addition to the types we have also seen the original of Pervinquière 1907, pl. 11, fig. 16*a–b*, from Sidi Youssef, Tunisia, now in the collections of the Sorbonne, and refigured here as pl. 60, figs. 7–8.

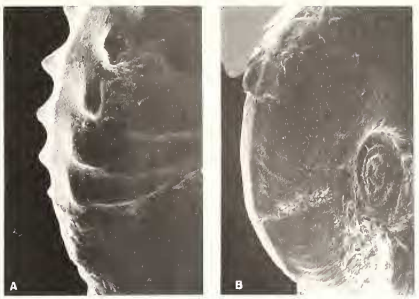
Description. A subspecies of *A. boghariense* in which the umbilical bullae are fine and regular. There is a total of about fifty ribs per whorl.

Occurrence. Lower Cenomanian of Algeria and Tunisia, according to the records of Pervinquière (1907).

Algericeras (*Algericeras*) *boghariense paucicostatum* subsp. nov.

Plate 60, figs. 9–19, 27–29; text-figs. 1*c*, 3*j–l*; 4*a*

1907 *Mortoniceras proratum* Coq.; Pervinquière, p. 237 (*pars*), pl. 11, figs. 10–12 only.
1910 *Mortoniceras* (?) *proratum* Coquand; Pervinquière, p. 66 (*pars*), pl. 15, figs. 27–28.
1979 *Prionocycloides* sp. cf. *proratum* (Coquand, 1880); Young, p. 38, pl. 1, figs. 55–59, 67–69; text-figs. 9*c*, 10*a*.



TEXT-FIG. 4. Serrated ventral keel in *Algericas*. A, *A.* (*A.*) *boghariense paucicostatum* subsp. nov.; B, *A.* (*A.*) *proratus* (Coquand). Magnification: A, × 10; B, × 7.5.

Holotype. The original of Pervinquière 1907, pl. 11, fig. 11*a–b*, refigured here as our Pl. 61, figs. 14–16, from the Lower Cenomanian of Si Abd el Kerim, Tunisia. Other specimens studied: The originals of Pervinquière 1907, pl. 11, fig. 10*a–b* from Guern er Rhezal; figs. 11*a–b* and 12, from Si Abd el Kerim; Pervinquière 1910, pl. 15, figs. 27, 28*a–c*, from Berrouaghia, Algeria. Two specimens in the MNHP, from Aumale, Algeria. Unless otherwise indicated, all specimens are in the Sorbonne Collections.

Diagnosis. A subspecies of *A. boghariense* in which umbilical tubercles tend to strengthen on alternate primary ribs. The total number of ribs is thirty-five to forty per whorl.

Discussion. The diagnosis adequately characterizes this subspecies; representative sutures are shown in text-figs. 1*c*, 3*j–l*. The strong ornament distinguishes this form from the nominate subspecies, and also from *A.* (*A.*) *proratum*. There are closer similarities to *A.* (*A.*) *numidicum* (Sornay) (1955, p. 31, pl. 2, figs. 15–15*a*), but there the ribs are flexuous and more robust and arise in groups from the umbilical bullae. The suture is highly simplified.

Occurrence. Lower Cenomanian of Algeria, Tunisia and Chihuahua Province, Mexico.

Algericeras (*Algericeras*) *proratum* (Coquand)

Plate 60, figs. 1–5, 20–21, 33; text-figs. 3*h*, *i*, 4*b*

1879 *Ammonites proratus* Coquand, p. 32.
1907 *Mortoniceras proratum* Coquand; Pervinquière, p. 237, pl. 11, figs. 5–9 (*non* figs. 10–12 = *Algericeras boghariense paucicostatum* nov.); text-fig. 97 only.
1910 *Mortoniceras proratum* Coquand; Pervinquière, p. 66, pl. 15, figs. 20–26 only (*non* figs. 27, 28 = *Algericeras boghariense paucicostatum* nov).
1925 *Prionocycloides proratus* (Coquand); Spath, p. 182.
1928 *Mortoniceras proratum* Coquand; Collignon, p. 47.
?1931 *Schloenbachia* (*Inflaticeras*) aff. *boghariense* Coquand; Collignon, p. 35, pl. 3, figs. 19–19*b*.
1933 *Prionocycloides proratus* (Coquand); Spath, p. 437.
1957 *Prionocycloides proratus* (Coquand); Wright, p. L 400, fig. 519, 5.
non 1964 *Prionocycloides proratus* Coq.; Collignon, p. 22, pl. 322, figs. 1422–3 (= *Algericeras* (*Sakondryella*) *remolinense* (Böse)).

Types. The syntypes are the three specimens in the Coquand Collection, now in Budapest, figured by Pervinquière in 1910 (pl. 15, figs. 20–22).

Material studied. The originals of Pervinquière 1907, pl. 11, figs. 6–9, from Guern er Rhezal, Tunisia. The originals of Pervinquière 1910, pl. 15, figs. 25–26, from Aumaule, Algeria. Four additional specimens from Guern er Rhezal and six from Aumaule. All in the Sorbonne collections.

Description. Only minute pyritic specimens are known; they appear to be phragmocones of a genuinely dwarf species, for in some specimens the sutures are beginning to approximate. The coiling is rather involute, with a compressed whorl section, slightly convex flanks, and a rounded to subtabulate venter with a keel that is at first nodate but soon becomes entire, rather sharp, and bordered by distinct furrows. Feeble, oblique, biconcave primary ribs with or without distinct comma-shaped bullae arise on the umbilical margin, have one or two feeble branches low on the sides and again three-quarters of the way up. All ribs bear a very slight ventral tubercle; at first they may cross the venter in a chevron, raised into a siphonal node, but later, when the keel is entire, they end at the shoulders. The suture (text-fig. 3*h*) has a broadly bifid E/L, rather feebly indented L, with three or four simple indentations, and three additional minor lobes to the external suture, the innermost of which tends to be entire.

Discussion. Pervinquière included in the present species a few strongly ribbed specimens. These, however, are more evolute, have flat sides, and their ribs branch only once, low on the side. They are best referred to *A*. (*A*.) *bogharíense*. Spath (1925) in establishing *Prionocycloides* and *Algericeras*, did not explain the differences between his genera or their type species. In fact Coquand's *Ammonites proratus* and *boghariensis* are closely related in their size, compressed form, initially nodate keel becoming entire and the general arrangement of the suture. *Am. proratus* differs in its higher, less flat-sided whorl section, greater degree of involution, much finer, weaker, and bidichotomous ribbing, and its rather more indented and less pseudoceratitic suture.

Occurrence. Early Cenomanian of Algeria and Tunisia, according to the records of Dubourdieu (1953), rather than the 'Vraconnien' date originally given it by Pervinquière. The species may also occur at the same level in Madagascar.

Subgenus SAKONDRYELLA Collignon, 1964

Type species. *Euhystrichoceras* (*Sakondryella*) *madagascariensis* Collignon, 1964 p. 21, pl. 322, figs. 1412–1421 by original designation = *Euhystrichoceras remolinense* Böse, 1928, p. 247, pl. 9, figs. 13–15.

Diagnosis. Moderately compressed to inflated *Algericeras* in which the keel is nodate throughout.

Occurrence. Early Cenomanian of Madagascar and Coahuila, Mexico.

Algericeras (*Sakondryella*) *remolinense* Böse

Plate 61, figs. 1–33; text-fig. 3*a–g*.

1928 *Euhystrichoceras remolinense* Böse, p. 247, pl. 9, figs. 13–15.
1964 *Euhystrichoceras* (*Sakondryella*) *madagascariensis* Collignon, p. 21, pl. 322, figs. 1412–1421.
1964 *Prionocycloides besairei* Collignon, p. 22, pl. 322, fig. 1424.
1964 *Prionocycloides proratus* Coquand; Collignon, p. 22, pl. 322, figs. 1422–3.
1979 *Euhystrichoceras remolinense* Böse, 1928; Young, p. 35, pl. 2, figs. 4–5, text-fig. 11*d*.

Holotype. UCBS—8226, from the Lower Cenomanian Buda Limestone of El Remolino, 2 km from Rio San Rodrigo in a dry canyon near the road to Oregano, near Jimenez, Coahuila, Mexico, refigured here as Pl. 61, figs. 1–3. A cast of this specimen is in the collections of the British Museum (Natural History), no. C35764.

EXPLANATION OF PLATE 61

Figs. 1–33. *Euhystrichoceras* (*Sakondryella*) *remolinense* Böse. 1–3, UCBS 8226, the holotype, from the early Cenomanian Buda Limestone of El Remolino, near Jimenez, Coahuila, Mexico. 4–6, MC 1412, the holotype of *E*. (*S*.) *madagascariense* Collignon; 7–9, MC 1421, the inflated var. d of Collignon; 10–12, MC 1417, var. a; 13–15, MC 1420, var. c; 16–18, MC 1418, var. b; 19–21, MC MC1419, var. c; 23–33, partial ontogenetic series; 22–24, MC 1413; 25–27, MC 1414; 28–30, MC 1415; 31–33, MC 1416. All specimens except the holotype are limonitic phragmocones from the early Cenomanian of Collignon's (1964) locality 478, Beraketa sur Sakondry (Manera), Madagascar. 1–3 are figured × 1; 4–33 are × 2.

KENNEDY and WRIGHT, *Euhystrichoceras* (*Sakondryella*)

Other specimens studied. The holotype of *E.* (*S.*) *madagascariense*, MC 1412, and 400 other paratype specimens from the Lower Cenomanian of Collignon's (1964) locality 478, 5 km west of Beraketa sur Sakondry (Manera), Madagascar.

Dimensions

	D	*Wb*	*Wh*	*Wb: Wh*	*U*	*B*	*R*
MC 1421 (var. a)	18·0 (100)	11·2 (62)	6·8 (38)	1·64	5·1 (28)	11	33
MC 1412 (type)	19·0 (100)	9·0 (47)	6·8 (36)	1·32	5·4 (28)		
MC 1413	16·8 (100)	8·3 (49)	5·8 (34)	1·43	4·1 (24)	12	32
MC 1414	12·8 (100)	6·4 (50)	4·6 (36)	1·39	3·4 (27)	12	31/32
MC 1417 (var. a)	18·8 (100)	8·8 (47)	8·5 (45)	1·04	5·1 (27)	12	36
MC 1418 (var. b)	17·6 (100)	8·0 (45)	7·8 (44)	1·02	5·8 (33)		36
MC 1419 (var. c)	17·3 (100)	7·0 (40)	8·0 (46)	0·875	4·8 (27)		
MC 1420 (var. d)	19·0 (100)	7·8 (41)	7·8 (41)	1·0	5·2 (27)		

Description. The holotype of *A.* (*Sakondryella*) *remolinense* is the largest individual known, being some 34 mm in maximum diameter. It is a fairly well preserved but slightly distorted limestone mould. The description that follows is based largely on the abundant Madagascan material, which is in the form of adult and juvenile limonitic phragmocones. As Collignon (1964, p. 21) notes, this shows great variation (Pl. 61, figs. 4–33). In the typical form (Pl. 61, figs. 4–6), the coiling is moderately evolute, with a quite deep umbilicus. The umbilical wall is rounded and merges imperceptibly with the strongly rounded inner flank. The whorl section is depressed and rounded in intercostal section, with the greatest breadth close to mid-flank (text-fig. 3*b*). The costal section is more angular, rounded-polygonal, with the greatest breadth at the umbilical bullae, when these are developed. Ornament consists of nine strong umbilical bullae on the outer whorl at a diameter of approximately 20 mm; these become increasingly prominent as diameter increases. Ribs arise in pairs from the bullae, whilst there are also occasional additional single ribs arising at the umbilical shoulder. Additional single intercalated ribs arise at mid-flank, to give a total of thirty-one to thirty-two per whorl. The ribs are prorsiradiate and very slightly flexed, convex on the inner flank but straight at mid-flank. Each terminates in a small rounded oblique ventral tubercle, separated by a smooth band from a corresponding number of aperturally displaced, rounded siphonal clavi sited on a weak siphonal ridge.

These forms are connected by intermediates to individuals with much flatter sides (Collignon's (1964) var. *a*). These have a subtrapezoidal whorl section and feebler bullae (Pl. 61, figs. 10–11) up to thirty-six ribs per whorl, branching high on the flanks, with more single ribs and one or two intercalatories. Increasing compression leads to individuals like those shown as Pl. 61, figs. 13–21 (Collignon's vars. b and c), with whorl breadth to height ratios of as little as 0·85 (as compared with 1·32 in the typical form); bullae weaken and there are up to forty ribs per whorl, arising in groups of up to three from the bullae with additional single long ribs and intercalatories. The siphonal clavi are prominent and merge into a serrated keel in the slenderest individuals. The other extreme variation (Collignon's var. d) has, in contrast, whorl breadth to height ratios of up to 1·7 (Pl. 61, figs. 7–9). Bullae are massive, giving rise to groups of relatively coarse ribs with additional intercalatories; there are seven to nine bullae per whorl, corresponding to thirty-two to thirty-four ribs. In all variants the suture is of the same basically simple pattern (text-fig. 3*a*, *c*, *d*, *g*). E is relatively deep with long, simple prongs and a little divided median element. E/L is bifid, usually asymmetric, with minor incisions. L is narrow and simple, U_2 broad and asymmetrically bifid.

Discussion. Restudy of the holotype of *Euhystrichoceras remolinense* shows that the keel, described by Böse (1928, p. 248) as being largely broken, in fact bears distinct clavi (Pl. 61, fig. 1) on a continuous ridge (Pl. 61, fig. 3), that the ribs terminate in oblique clavi (Pl. 61, fig. 3), and that there are well-developed bullae giving rise to groups of branching and intercalated ribs (Pl. 61, fig. 2). Although poorly preserved, such of the inner whorls as are visible compare well with those of the more inflated forms in the Madagascan collection (Pl. 61, figs. 4–9, 25–33). We conclude that the two species are synonymous. Böse's name has priority. We would further suggest that *Prionocycloides besairei* Collignon (1964, p. 22, pl. 322), which is from the same horizon and locality as the *Sakondryella* population, is also a synonym, representing the compressed end of the variation series. The presence of siphonal clavi distinguishes this species from *Euhystrichoceras* species, although we note the minute crenulations seen on the shell in specimens of *E.* (*E.*) *adkinsi* (see p. 422).

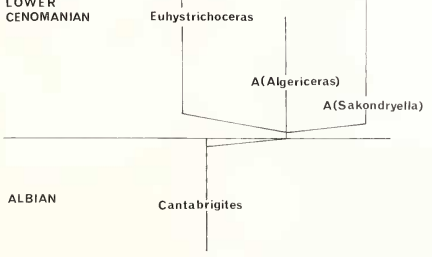
Occurrence. Lower Cenomanian of Madagascar and Coahuila Province, Mexico.

PHYLOGENETIC CONCLUSIONS

In seeking for probable ancestors for the ammonites considered here, the obvious source is in the keeled forms with simplifying sutures from the Uppermost Albian *Stoliczkaia dispar* Zone. Such are the species of *Cantabrigites* and the various poorly known species referred to *Spathiceras*, all of which appear to be either *Cantabrigites* or *Hysteroceras*. Spath (1933, p. 437) had already considered the possibility of a close relationship between *Cantabrigites* and *Algericeras* and *Prionocycloides* but, as indicated above, seems to have concluded, though his words are not at all clear, that the African genera were closer to *Schloenbachia*. Against such a link is the fact that there are no *Schloenbachia* that show signs of a simplifying suture, whereas *Cantabrigites* does (text-fig. 1*b*, *d*). It is much easier to derive the suture of *Algericeras* or *Euhystrichoceras* from that of *Cantabrigites* (e.g. Spath 1933, pl. 45, fig. 4; pl. 46, fig. 11*a–b*; text-fig. 1*a–d*) than from those of *Schloenbachia*; the increase in number of elements by subdivision around the umbilical seam is a natural concomitant of the higher, more compressed whorl section. Although *Cantabrigites* are always more evolute than *Algericeras*, comparison of Pl. 60, figs. 1–24, 27–29 and Pl. 60, figs. 31–32, 34–40 shows that comparable styles of ribbing develop in the two genera in the case of at least some individuals. However, the development of a finely crenulate keel in *Algericeras sensu stricto* has no analogue in *Cantabrigites* so far as is known, and represents a new departure for the group.

This relationship is supported by known stratigraphical records; *Cantabrigites* characterizes all of the late Albian *dispar* Zone; *A.* (*Algericeras*) first appears as a rarity at the Albian/Cenomanian boundary (e.g. *A.* (*A.*) [*Prionocycloides*] *numidicus* (Sornay) (1955, p. 31, pl. 2, fig. 15)) according to the careful records of Dubourdieu (1956), but is commonest in the lowest Cenomanian. *Algericeras* (*Sakondryella*) appears to be a later, paedomorphic derivative in which the juvenile nodate keel has developed into siphonal clavi which are retained to maturity. The reliably dated Mexican occurrence in the Buda Limestone is well above the base of the Cenomanian as recently defined by Mancini (1979). The Madagascan material is associated with a very rich fauna listed in Besairie and Collignon (1972, p. 364), but appears to be stratigraphically mixed, with more than one horizon represented, although low in the Lower Cenomanian.

Euhystrichoceras is said to occur at a slightly higher level in the Lower Cenomanian of Tunisia according to Dubourdieu (1956), although it occurs in the earliest Cenomanian faunas recognized in England and France. In Texas it occurs above the Buda Limestone which yields *Algericeras* (*Sakondryella*); for this reason it may perhaps be a derivative of *Algericeras*, rather than directly



TEXT-FIG. 5. Suggested phylogeny of *Euhystrichoceras* and *Algericeras*.

from *Cantabrigites*, for which there is little evidence in terms of ornament. We would draw particular attention to *A.* (*Algericeras*) *numidicum* (Sornay) (already referred to above) as a possible intermediate: this species already possesses flexuous ribs arising in groups from bullae and a more rounded whorl than either *A.* (*Algericeras*) or *Cantabrigites*. That there is a gap of more than half the Cenomanian between Lower and Upper Cenomanian occurrences of *Euhystrichoceras* indicates how little is known of the full history of this genus.

Another group of diminutive keeled ammonites from the *dispar* Zone has usually been referred to *Spathiceras* Whitehouse, 1927, which has sometimes also been recorded from the Cenomanian. As discussed by Cooper and Kennedy (1979), the type species is in fact from the low Upper Albian and the genus is probably a junior synonym of *Hysteroceras*, to which the *dispar* Zone forms may also belong. The ribbing style is, however, quite distinct from that of the other genera discussed here, and small size alone gives rise to the superficial similarities. The inferred phylogeny of these last Upper Cretaceous mortoniceratines is summarized in text-fig. 5.

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